

A Dynamic Model of Cotton Emergence Based on the Thermal Dependence of Malate Synthase

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ABSTRACT

Cotton (*Gossypium hirsutum* L.) is frequently planted when temperatures are not optimal for germination and emergence. Delayed emergence, a common contributor to diminished plant performance later in the season, is often related to nonoptimal temperatures. Improvement of cotton performance requires knowledge of the source, pattern, and magnitude of thermal limitations on seedling metabolism. In this study the thermal dependence of malate synthase, an enzyme involved in cotton seedling lipid metabolism, was used to define the pattern and magnitude of thermal limitations and as the basis of a metabolic model to predict emergence under variable temperatures in the field. Soil temperature at seed depth was monitored over the cotton-planting season of 2005 and characterized as optimal, suboptimal, and supraoptimal. Suboptimal temperatures were common and supraoptimal temperatures were less frequent. A metabolic model to predict emergence was developed and the predicted emergence was in agreement with a widely used degree-day based model. Metabolic indicators of thermal optimality may prove useful in studies of seedling responses to thermal variation.

ENVIRONMENTAL TEMPERATURE is a major determinant in plant production. The effects of adverse temperatures limit crop yield and quality worldwide. Thermal variation is an inevitable aspect of life for crops and in many regions crops must be grown in the interval between lethally low temperatures that bound the growing season. On the High Plains of Texas, early season low temperatures can be avoided for cotton by planting in the late spring though late planting dates often expose the plant to end-of-season low temperatures that adversely affect yield and quality. While earlier plantings reduce the chance that low temperatures at the end of the season will adversely affect yield or quality, they increase the potential for seedlings to be exposed to early season low temperatures. Thus both early and late plantings of cotton can result in low temperature stress to the plant with potentially damaging consequences. Given these competing interests what is the producer to do? Apparently, plant early. Replanting a cotton crop due to early-season low temperature damage, while certainly undesirable, potentially entails less cost than the reductions in yield and quality that result from adverse

temperatures at the end of the season when input costs have accumulated to high levels. This simple fact leads to an ongoing interest in early planting dates for cotton on the Southern High Plains of Texas.

The effects of suboptimal temperatures on the germination and emergence of cotton seedlings are numerous (Meryl et al., 1986; Wanjura et al., 1969). Rapid seedling emergence is desirable since the health and vigor of seedlings is often correlated with the time required for the seedling to emerge after planting (Wanjura et al., 1970; Kerby et al., 1989; Steiner and Jacobsen, 1992).

Wanjura and Buxton (1972) used hypocotyl elongation to characterize the effects of thermal variation on emergence of cotton seedlings. While empirically based models are widely used in predicting temperature effects on cotton emergence (Boman and Lemon, 2005), they often require adjustment to account for regional variation in production systems.

Mahan (2000) investigated the relationship between the thermal dependence of enzyme metabolism and seedling emergence in cotton and sunflower (*Helianthus annuus* L.) at constant temperatures. Malate synthase was extracted from germinated seed and the thermal dependencies of the apparent Michaelis–Menten constant (K_m) maximum velocity (V_{max}) were determined. Apparent K_m and V_{max} were used as inputs into the Michaelis–Menten equation which predicted reaction velocity at subsaturating substrate concentrations thought to be representative of in vivo conditions across a range of temperatures. The analysis indicated that the thermal dependence of malate synthase velocity, as predicted from the thermal dependencies of maximal velocity and apparent K_m , was sufficient to predict seedling emergence over a range of constant temperatures. It was suggested that the estimated in vivo activity of the enzyme at a given temperature was an effective predictor of overall seedling response to temperature. The ability to predict emergence rates of seedlings at a variety of constant temperatures on the basis of the thermal dependence of enzyme function suggested an approach to the analysis of performance under variable temperatures. The use of a metabolically-based definition of thermal optimality provides the opportunity to categorize the thermal environment with respect to metabolic rates that are mechanistically linked with seedling performance. It is anticipated that plants with enhanced low temperature metabolism, while potentially better suited to low temperature growth might, as a consequence, be subject to diminished performance at higher temperatures.

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Abbreviations: DOY, day of year; PPP, potential planting period.

To our knowledge, no enzymatically-based mechanistic model of temperature effects on cotton emergence under variable temperature conditions in the field has been described. The goal of the present study was to use the thermal dependence of the enzyme malate synthase from cotton to characterize the occurrence of suboptimal, optimal, and supraoptimal temperatures over range of possible planting dates and thermal environments on the Southern High Plains of Texas. The four approaches used in this study were: (i) to define suboptimal, optimal, and supraoptimal temperatures in cotton seedlings with respect to the thermal dependence of malate synthase velocity; (ii) to categorize the thermal variation over various planting periods as suboptimal, optimal, or supraoptimal; (iii) to model the cumulative product of malate synthase over various planting periods to determine the contributions of suboptimal, optimal, and supraoptimal temperatures to the amount of product produced by malate synthase; (iv) to develop a predictive tool for seedling emergence based on the thermal dependence of malate synthase velocity. Two soil surface treatments were incorporated in an effort to assess the effect of modification of soil temperature on seedling performance.

MATERIALS AND METHODS

Plant Material

Cotton (cv. Paymaster 958) was planted on day of year (DOY) 115 (25 April) and DOY 131 (11 May) in 2005. Seedbeds were prepared on 1 m row spacing. A pre-plant irrigation provided sufficient moisture for seedling establishment.

Soil Surface Treatments

Two soil surface treatments were established; brown (BN) consisting of a bare soil surface and black (BK) that was darkened by applications of an aqueous carbon black suspension (100 g/L Aqueous Carbon Black Dispersion #KDR-6214E, Kennebec Color Company Inc., Arlington, TX). This treatment was reapplied as needed following rain events.

Soil Temperature Monitoring

Soil temperature was monitored at 5 and 10 cm below the soil surface with a thermistor temperature probe (TMCx-HD Onset Computer). The temperature was measured every 5 min and collected with a data logger (U12 data logger Onset Computer) from DOY 115 through DOY 182.

Seedling Emergence

The number of emerged seedlings was determined daily beginning with the first emerged seedling and continuing until the number of emerged seedlings was constant. The emerged seedlings were measured in five subplots of 10 m length. The first seedlings emerged 10 and 4 d after planting in the DOY 115 and DOY 131 plantings, respectively.

Enzyme Thermal Dependence

The relationship between the activity of the enzyme malate synthase and the rate of emergence was established for cotton and sunflower by Mahan (2000). In the germinating seed/seedling, the conversion of stored lipid into carbohydrates

provides energy for growth and the velocity of malate synthase reaction over time (amount of product produced) is related to the production of carbohydrate for growth-related metabolism. In this scheme the cumulative velocity of the enzyme over time is used as an indicator of conversion of lipid into carbohydrate and ultimately growth. Mahan (2000) developed a kinetic model of the thermal dependence of the enzyme malate synthase from cotton and sunflower seedlings based on the thermal dependencies of apparent K_m and V_{max} . It was demonstrated that the modeled thermal dependence was a predictor of the thermal dependence of seedling emergence rates across a 15 to 40°C range. At each temperature the Michaelis-Menten equation was solved for velocity using the measured values of apparent K_m and maximal velocity and setting the substrate concentration equal to the minimum observed value of the apparent K_m as previously described by Mahan (1994). A justification of this value follows in the results section. The predicted velocity of malate synthase as a function of temperature is shown in Fig. 1.

Emergence Prediction

In a study of cotton emergence at constant temperatures, it was demonstrated that at 30°C cotton emergence would occur in 72 h (Mahan, 2000). The thermal dependence of malate synthase at a 5°C interval (Fig. 1) was used to develop a model to predict seedling emergence under thermal variation. In the present work, multiplying reaction velocity (mol/h) at 30°C by 72 h, the amount of malate synthase product associated with emergence was calculated. This value was then used as the threshold product amount associated with emergence. To predict the effect of temperature on emergence in the field, the measured soil temperature at seedling depth (Fig. 2A) was used to calculate malate synthase product accumulation over time. The time required to accumulate the threshold product amount was used as the "time to 50% emergence" for that

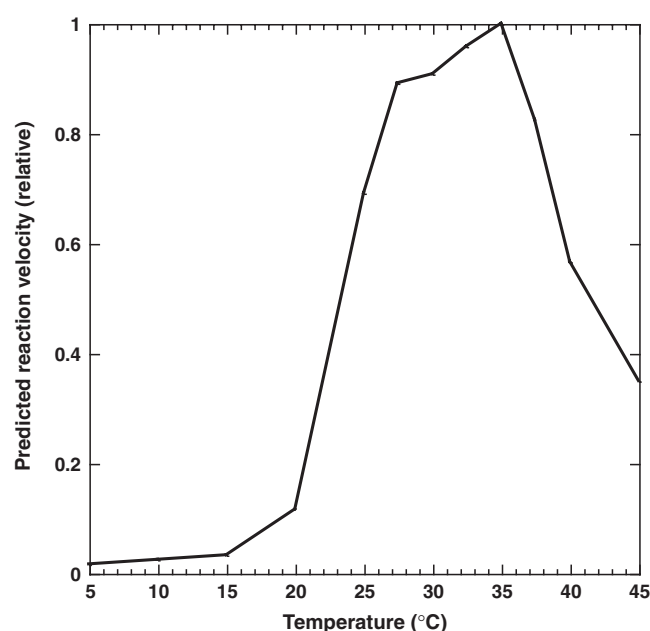


Fig. 1. The thermal dependence of malate synthase velocity predicted from thermal dependencies of apparent K_m and maximal velocity. Substrate concentration for velocity prediction was equal to minimum observed apparent K_m (substrate was not saturating). Figure modified from Mahan (2000).

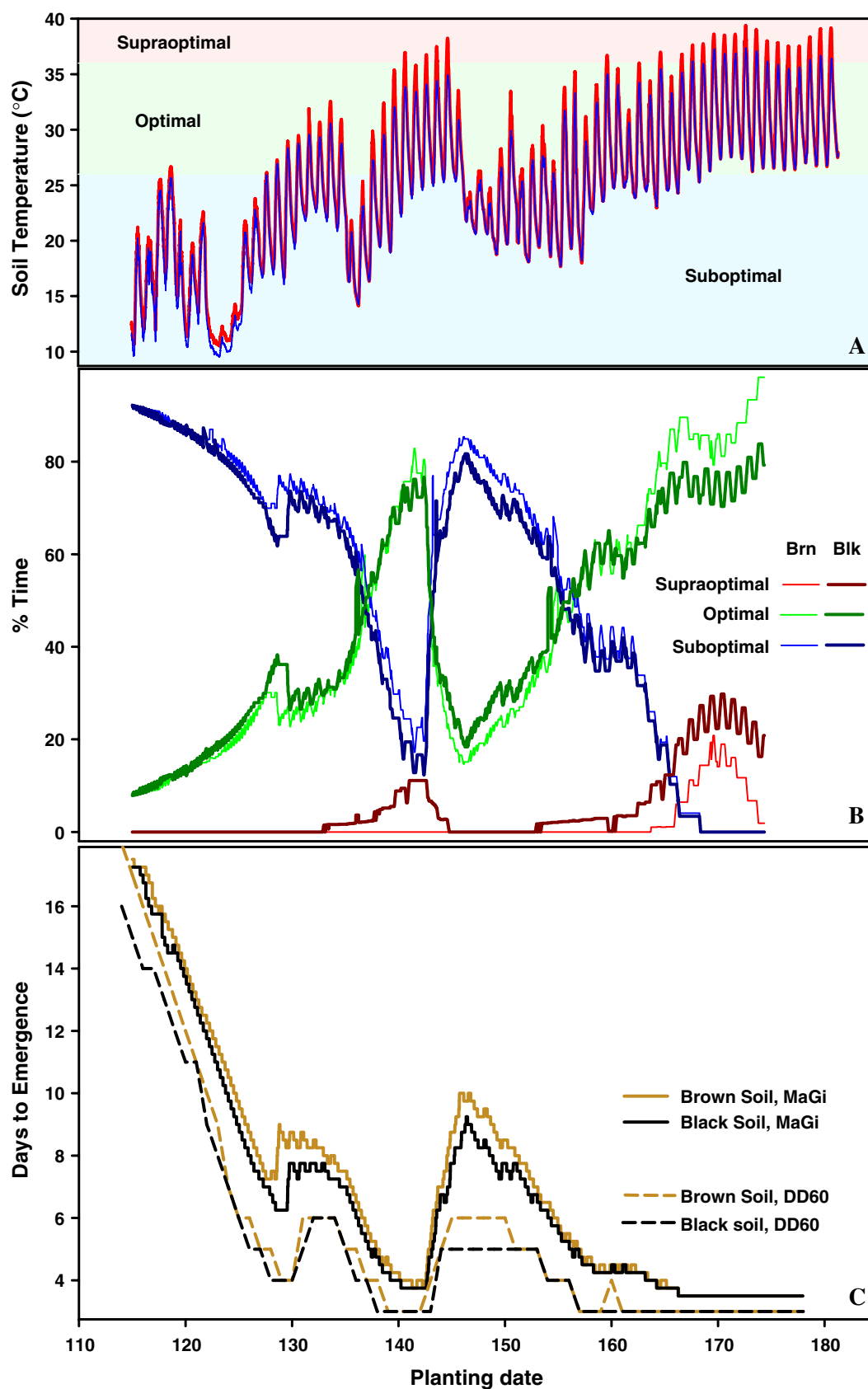


Fig. 2. Inputs (soil temperatures), Predicted time developing seedlings spend at suboptimal, optimal, or supraoptimal temperatures, and the modeled emergence time from planting. (A) Pattern of soil temperature at 5-cm depth for the period DOY 115 through DOY 180. Red, green, and blue backgrounds indicate temperatures defined as supraoptimal, optimal, and suboptimal temperatures, respectively. Black bars show potential planting periods A, B, C, and D used in analysis. (B) Distribution of temperature regimes experienced by developing cotton seedlings from planting to predicted emergence. (C) Predicted time from planting to emergence for cotton as determined from the malate synthase based model (MaGi), compared to a model based on accumulated heat units (DD60).

planting date. The time to emergence was predicted for planting at any date over the experimental interval (DOY 115–182).

An empirical model for cotton emergence (DD60 model) was used to predict emergence (Boman and Lemon, 2005). A base temperature of 15.5°C (60°F) was used with accumulation of 70 heat units required for emergence. Emergence time was calculated for planting dates over the experimental interval (DOY 115–182).

Potential Planting Periods

The experimental interval was divided into a series of 14-d potential planting periods (PPPs) for analysis of seedling/temperature interactions. A series of four sequential PPPs were generated spanning the period from DOY 126 to 182. The PPPs were identified by a letter and the DOY of the first day of the period that is, A126, B140, C154, and D168. The PPPs span a time period from a typical planting date of early May through 17 June which would be outside the range of potential planting dates for cotton on the Southern High Plains of Texas.

Frequency of Temperature

The frequency of temperature at 1°C intervals (as a percentage of time) during each PPP was determined for each treatment. The frequency of each temperature during each PPP was multiplied by the modeled velocity of malate synthase at that temperature to estimate the amount of product that could have been produced at each temperature over the course of the PPP.

RESULTS

Definition of Suboptimal, Optimal, and Supraoptimal Temperatures in Cotton

While the characterization of temperatures in terms of optimal and stressful (either high or low) is inherently subjective, such characterizations can be useful in the analysis of plant responses to temperature by providing a means of assessing the effect of thermal variation on the metabolism of the plant. The characterization of temperatures as suboptimal, optimal, and supraoptimal is most appropriately based on the plant function to be evaluated. In this study, the thermal velocity of a cotton seedling enzyme is being used to define the limits of optimal temperature in the developing seedling. The thermal dependence of malate synthase velocity used to define thermal stress in this study that has two distinct peaks (Fig. 1) resulting from two components of the thermal dependence of the enzyme. The peak at 28°C is a reflection of the thermal dependence of the apparent K_m and the peak at 35°C is indicative of the thermal dependence of maximal velocity at saturating substrate concentrations. The thermal dependence of the velocity is comparatively stable between 28 and 35°C with a more pronounced temperature effect above and below that range. Based on the observed thermal dependence of malate synthase velocity (Fig. 1), low, optimal, and high temperatures were defined as <26°, 26° to 36°, and >37°C, respectively. Though these delineations of optimal temperatures are not strictly quantitative, they were instructive in efforts to assess the effects of thermal stress on plants.

Categorization of the Thermal Environment

The soil temperature was monitored at 5 cm below the surface every 5 min over the experimental interval from DOY 115 to 182 (soil temperature measured at 10 cm below the surface was used to calculate values for missing data points at various points in the study). Temperature varied over the period with a general trend from lower to higher temperatures punctuated with transient periods of cooling and warming (Fig. 2A). The timing of the PPPs over the experimental interval is shown as well. Minimum, maximum, and mean temperatures for the various PPPs and soil surface treatments are listed in Table 1. The PPPs (A–D) show a general trend of increasing mean temperatures in both the brown and black treatments at the 5-cm depth. The application of carbon black to the soil surface increased the maximal daily temperatures as compared to the bare soil, although the magnitude of the increase was usually <4°C. Mean temperature was the same or slightly increased (1°C) between the brown and black soil treatments. Minimum temperatures were not affected by the soil surface treatment.

The fraction of temperatures that are categorized as optimal, suboptimal, and supraoptimal varied among the PPPs (Table 2). With respect to optimality, temperatures in the brown soil treatment were suboptimal for almost 50% of the time in the three earliest PPPs and only 2% in the final PPP. There was no time at supraoptimal temperatures in any PPP in the brown soil treatment. The black soil treatment, which was generally warmer than the brown treatment, exhibited a similar pattern of decreasing proportion of suboptimal temperatures with delayed PPPs. However unlike the brown soil treatment, in all but the first PPP there were temperatures that were classified as supraoptimal. The fraction of temperatures in the supraoptimal category was relatively small (1 and 5%). It should be noted that the last PPP was initiated on DOY 168 which would generally be beyond the planting date for cotton in the Southern High Plains of Texas. The results indicate that temperatures may be suboptimal for a majority of time even at planting dates that would typically be considered “normal” for cotton on the Southern High Plains of Texas. This analysis suggests that supraoptimal temperatures are not important limiters of cotton seedling emergence, even at later-than-normal planting dates.

Modeling the Cumulative Product of Malate Synthase Activity

The temperature distributions of suboptimal, optimal, and supraoptimal categories indicated that in the early

Table 1. Soil temperature during experimental interval. Brown is untreated soil surface and black is soil surface treated with carbon black.

Potential planting period	Brown			Black		
	Min.	Max.	Mean	Min.	Max.	Mean
	°C					
A (126)	14	32	23	14	35	24
B (140)	18	35	25	18	38	26
C (154)	18	36	27	18	37	27
D (168)	25	37	31	25	39	32

Table 2. Categorization of soil temperatures as suboptimal (<26°C), optimal (26–36°C), and supraoptimal (>37°C). Fraction of time that soil temperature at the 5-cm depth was within each category during the potential planting period. Numbers in parentheses indicate initial date in period as day of year. Brown is untreated soil surface and black is soil surface treated with carbon black.

Potential planting period	Brown			Black		
	Suboptimal	Optimal	Supraoptimal	Suboptimal	Optimal	Supraoptimal
A (126)	0.72	0.28	0.00	0.68	0.32	0.00
B (140)	0.66	0.34	0.00	0.58	0.41	0.01
C (154)	0.49	0.51	0.00	0.45	0.54	0.01
D (168)	0.02	0.98	0.00	0.01	0.94	0.05

PPPs suboptimal temperatures comprised a majority of the time. The amount of malate synthase product that was modeled to be produced at suboptimal, optimal, and supraoptimal temperatures was calculated (Table 3). The total enzyme product produced during each PPP increased from the earlier to later PPP. The theoretical, or modeled, increases in potential product from earliest to latest PPPs were 2.5 and 2.2-fold respectively in the brown and black treatments. In the brown soil treatment, during the first and second PPPs, 35% of the product was produced under suboptimal temperatures with the remainder attributable to optimal temperature accumulations. In the third PPP the amount of product produced at suboptimal temperatures was 23% and by the last PPP only 1% of product was produced at suboptimal temperatures. In the brown soil treatment there were no supraoptimal temperatures and thus no product produced at supraoptimal temperatures. The application of carbon black to the soil surface in the black soil treatment resulted in an increase in temperatures that resulted in some changes in the fraction of total product produced under suboptimal temperatures. In the first and second PPPs, approximately 30% of the product was produced under suboptimal temperatures. Suboptimal temperatures accounted for 20% of the accumulated product in the third PPP and only 6% in the final PPP.

Development of a Predictive Tool for Seedling Emergence

Temperature over the experimental interval in the study was typically variable with a seasonal trend of increasing temperatures punctuated with events of rapid temperature declines and subsequent warming. The analysis of the thermal environment over the various PPPs indicated that temperature could be characterized as variously suboptimal and optimal with supraoptimal temperatures occurring only in the black soil treatment during the later PPPs. This approach provided very little insight into temperature limitations in the field and led

to an effort to assess the cumulative effect of temperature variation on seedling emergence. Hence, a model was developed to define the incremental accumulation of malate synthase product over time for the study interval.

This model used the thermal dependence of malate synthase (Fig. 1) to predict seedling emergence under thermal variation. It should be pointed out that Fig. 1 represents the results of modeled malate synthase activity based on a substrate concentration that is equal to the minimum K_m value. That in vivo substrate concentrations are often very similar to the minimum K_m value of an enzyme is well established both experimentally and theoretically (Hochachka and Somero, 1984). In the kinetic model that was used to generate Fig. 1, increasing substrate concentration results in a broadening of the thermal dependence of reaction velocity (J.R. Mahan, unpublished results, 2000). As substrate concentration increases the contribution of the thermal dependence of apparent K_m diminishes and the thermal dependence of reaction velocity is determined by the thermal dependence of V_{max} . The analysis of the 2005 planting season in Lubbock, TX is shown in Fig. 2C. The time to 50% emergence varied over the analytical interval with a minimum period of 3.5 d at DOY 166 and a maximum of 17 d at DOY 115. The black soil surface treatment resulted in predicted emergence times that were equal to or faster than the brown soil surface treatment. The average decrease in time to 50% emergence was 0.41 d with a minimum of 0 and a maximum of 2.75 (for a planting date of DOY 128).

The predicted emergence from the model was compared to measured emergence for two planting dates and with the emergence times predicted by a widely used model based on heat unit accumulation (Boman and Lemon, 2005). Cotton for emergence determinations was planted on DOY 115 and 131. The number of days required for 50% emergence was 14 in the DOY 115 planting and 7 in the DOY 131 planting. The measured emergence periods compare favorably with predicted emergence of 16 and 8 d from the emergence model

Table 3. Product accumulation at suboptimal, optimal, and supraoptimal soil temperatures at the 5-cm depth. Fraction of Total Product produced at temperatures suboptimal (<26°C), optimal (26–36°C), and supraoptimal (>37°C). Total product is predicted cumulative activity of malate synthase (relative units) during the potential planting period. Numbers in parentheses indicate initial date in period as day of year. Brown is untreated soil surface and black is soil surface treated with carbon black.

Potential planting period	Brown				Black			
	Suboptimal	Optimal	Supraoptimal	Total product	Suboptimal	Optimal	Supraoptimal	Total product
A (126)	0.35	0.65	0.00	87	0.31	0.69	0.00	95
B (140)	0.35	0.65	0.00	107	0.29	0.70	0.01	118
C (154)	0.23	0.77	0.00	141	0.20	0.89	0.01	147
D (168)	0.01	0.99	0.00	215	0.01	0.87	0.12	215

(82 and 87% of predicted for DOY 115 and 131 plantings, respectively). There was no clear difference in time required for 50% emergence associated with the brown or black soil treatments though the model predicted a difference of 0.25 and 0.5 d for the DOY 115 and 131 plantings. Emergence predicted by the degree-day based model (DD60, Fig. 2C) agrees well with the emergence predicted by the metabolic model (metabolic model, Fig. 2C) and indicates the potential utility of a metabolic approach to the analysis of the effect of temperature on cotton emergence.

DISCUSSION

Cotton on the Southern High Plains of Texas is often planted when temperatures are not optimal (Gipson, 1986); suboptimal temperatures are generally perceived as a greater problem than supraoptimal. While other factors, including seed quality, planting depth, and soil moisture have large effects on seedling emergence, temperature remains the major practical consideration in determining planting dates. Planting guidelines are most often empirically based on either field observations or analysis of the emergence of seedlings under controlled temperatures. In this study the thermal dependence of a metabolic enzyme from cotton seedlings (malate synthase) was used to develop a mechanistic tool that would allow a more quantitative approach to analysis of thermal limitations on seedling emergence.

The thermal dependence of malate synthase activity was used to delineate suboptimal and supraoptimal temperatures with respect to metabolic activity in the plants. The analysis of the temperature at a 5 cm soil depth with respect to the suboptimal and supraoptimal temperatures indicated that temperatures in all three categories were represented at some point over the analysis interval, though supraoptimal temperatures were very rare. Clearly, for cotton during the PPPs analyzed in this study, suboptimal temperatures had the greatest potential to adversely affect seedling performance. Treatment of the soil surface with carbon black resulted in warming of the soil but to a relatively small degree.

The modeled enzyme activity indicated that total product produced varied among the various PPPs analyzed. Comparison of the frequency of temperatures, classified as suboptimal, optimal, and supraoptimal, with the potential enzyme product produced within each class indicated that enzyme function at optimal temperatures accounted for an amount of product that was disproportional to the frequency of optimal temperatures over the potential plant periods (Table 3).

The metabolically-based model of thermal dependence of malate synthase predicted the number of days to 50% emergence for cotton over the experimental interval. The analysis predicted days to emergence for planting on any date based on the soil temperatures following the potential planting and the rate of accumulation of malate synthase product at those temperatures. The results describe a pattern of emergence times ranging from a maximum of 16 d at DOY 115 to a minimum of 3.5 d at DOY 165. Field emergence for two plantings in 2005 were

in agreement with predictions (predicted/measured 82% and 87% for DOY 115 and DOY 131 plantings). This approach defines the relationship between the thermal dependence of metabolism in the seedling and the thermal environment.

Historically there has been interest in the prediction of seedling emergence under variable environmental conditions. Various researchers have developed models that account for temperature effects on seedling emergence.

Wang (1960) reviewed the strengths and weaknesses inherent in heat unit approaches to plant responses including seedling emergence in a paper that is still relevant more than 40 yr later. Among the criticisms of heat unit approaches the limitation of a single threshold temperature was noted. One of the advantages of the model approach in this study is the use of a thermal response curve to assess plant response to temperature.

Roussopoulos et al. (1998) investigated the effects of controlled temperature on the growth and development of cotton. One of their suggestions was that models of plant temperature responses could be greatly improved by using smaller time and temperature intervals to describe plant responses. The model described in this paper can use time increments on the order of minutes as opposed to days as in many emergence models. The incorporation of a thermal response curve with a resolution of a degree or less can also improve the response to thermal variation over time.

Hammer et al. (2004) considered the difficulties inherent in attempts to incorporate molecular and cellular analyses of plants into understanding of plants at the whole plant and crop levels. They particularly note the complexity of environmental variation common in plants and the difficulties of adequately representing system dynamics in simple mathematical models. Appropriately defining the scale of operation within the simulated system is particularly challenging. Clearly the approach in this study was to bridge from an enzyme scale to a seedling scale with a rather simple, some would say simplistic, model approach. Clearly the approach in this study is capable of matching the predictions of commonly accepted empirical approaches to predict seedling emergence as a function of temperature within a variable environment. Its ultimate utility and/or superiority remains to be seen and will only be established through its use by others who are interested in modeling or modifying cotton seedling responses to temperature.

The utility of such a metabolic approach in understanding thermal behavior of seedling emergence is that it can be used to categorize the timing, duration, and severity of optimal and nonoptimal temperatures during the planting period. While, in this study, the thermal dependence of an enzyme involved in seedling metabolism was used to "drive" the model, the thermal dependence of other metabolic processes might prove useful as well. Moreover, analyses of the effects of altered thermal dependence (either naturally occurring or by transgenic modification) on the performance of the young plant under various temperature scenarios might be instructive. For example, one could model the effect of a few-degree shift in the thermal de-

pendence of the “driver” on seedling performance in different environments based on archival datasets.

CONCLUSIONS

The thermal dependence of the enzyme malate synthase appears to be a useful tool for defining thermal limitations on cotton emergence. A simple metabolic model, based on only two assumptions, was developed for emergence prediction. The model assumes: (i) that the rate of emergence was proportional to the rate of conversion of seed reserves as reflected in cumulative activity of the malate synthase in the seed and (ii) emergence of cotton at a constant temperature of 30°C occurs in 48 h. The metabolic model accounted for the broad trends in the DD60 empirical model and was more sensitive to fluctuations in temperature than the DD60 model. The agreement between predicted emergence from the metabolic and DD60 based models strongly supports the validity of a metabolic approach. Advantages of the metabolic-based model are that it provided higher thermal resolution (as evidenced by diurnal patterns of emergence progress), higher temporal resolution (maximal resolution of the degree-day model is 24 h) and it required limited empirical inputs.

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